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Foraminal structures of some Japanese species of the genera *Ammonia* and *Pararotalia*, family Rotaliidae (Foraminifera)

RITSUO NOMURA[1] **and YOKICHI TAKAYANAGI**[2]

[1] *Foraminiferal Laboratory, Faculty of Education, Shimane University, Matsue, 690-8504, Japan*

[2] *c/o Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai, 980-8578, Japan*

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Abstract. Rotaliid foraminifera have a complicated foraminal structure that has been recognized as the so-called toothplate. As to the interpretation of this toothplate, however, there has been confusion among foraminiferologists as to whether it is the same as the buliminid toothplate or not. In order to elucidate the apertural and foraminal structure, we examined some Japanese species of the genera *Ammonia* and *Pararotalia*.

The apertures of *Ammonia* and *Pararotalia* show fundamentally the same style of construction, but the resultant structures are different among species. We recognized two main components instead of the indefinite toothplate in the aperture: foraminal plate and umbilical coverplate. The foraminal plate constructed out of a foramen is a free structure of the bilamellar wall. This plate is originally formed in the final chamber where it delimits the posterior side of the final aperture. The umbilical coverplate closes the umbilical side of the preceding foramen. This coverplate is originally bilamellar and is continuous from the foraminal plate. Both the foraminal plate and umbilical coverplate are formed when the final chamber is constructed. The umbilical coverplate interconnects the new and preceding foraminal plate, which may lead to the original concept of toothplate. However, the umbilical coverplate is not associated with the final chamber wall, but assists in closing the umbilical side of the preceding chamber wall. Such a chamber construction is restricted to rotaliids, thus we reject the term toothplate as only indicating modified structures that pass through the aperture.

Descriptions of the rotaliid aperture are of value when we note the foraminal plate and umbilical coverplate. Thus two types of foramen, *Ammonia*-type and *Pararotalia*-type, were developed in the rotaliids.

Key words: aperture, foraminal plate, rotaliid foraminifera, taxonomy, toothplate.

Introduction

The toothplate is a characteristic structure developed in some taxa of benthic foraminifera (originally called "tooth pl ate", recently "toothplate"; e. g., Loeblich and Tappan, 1964, 1987). It has a varied morphology, usually manifested as a protruded free structure passing through the aperture. Before Hofker (1950, 1951a, b) recognized this structure as a useful systematic criterion of hyaline calcareous foraminifera, various distinctive parts of the aperture were called lip, tongue, tooth, partition and flap. Hofker's toothplate was regarded as a homologous structure with these variously named structures . Many forms having these apertural decorations have been classified into a number of families based on their apertural morphologies. Thus most hyaline calcareous foraminifera were included in Hofker's order Dentata (Hofker, 1951a). However, morphologically, some of these structures should be grouped together in the same category and some should be clearly differentiated from it. The toothplate concept includes so many forms of apertural complexity that rigid application of this term leads to ambiguous comparisons in systematics. In particular, the apertural complex of Hofker's Protoforaminata, the group having protoforamen, is different from that of his Deuteroforaminata, the group having both protoforamen and deuteroforamen.

In addition to such a confused recognition of the toothplate and related structures, development of the scanning electron microscopes (SEM) permitted the lamellar structure of the toothplate to be examined. The toothplate has been recognized as a bilamellar structure consisting of an inner lining and an outer lamella (Hansen and Reiss, 1971). However, the lamellarity is not consistent, since Revets (1993) suggested that the buliminid toothplate is made from the inner lining. Thus, the concept of toothplate is still confused among foraminiferal researchers in its structural and morphological aspects. The rotaliid toothplate is the best example of this, it being unclear whether it should be recognized as homologous with the buliminid toothplate or not on the basis of morphology and structure.

We describe the apertural and foraminal structures based on artificially dissected specimens and suggest the necessity of recognizing the morphological variation of the aperture.

Methods

Internal structure of foraminiferal test was examined by a scanning electron microscope using a hardened canada balsam (Nomura, 1983c). Some authors stress the importance of lamellar structure, particularly to the understanding of toothplate structure (e. g., Revets, 1989, 1993). In reconstructing the lamellar structure for the sectioned and etched specimens that have been embedded in epoxy resin we encountered difficulties, particularly for thinner walls. Alternatively, we etched the sectioned specimens with 0.5% phosphoric acid to observe the internal structure before removing the canada balsam. This method gives better results in interpreting the three-dimensional lamellar structures within walls.

Previous observations on the aperture of *Ammonia*

Earlier workers examined thin sections of foraminifera or examined the test with naturally broken walls to observe the toothplate. In this way, the toothplate of *Ammonia beccarii* (Linné), type species of the genus *Ammonia*, has been recognized as a free structure asymmetrically folded longitudinally and convex towards the umbilical side of the chamber (Hofker, 1950, 1951a, b; Reiss and Merling, 1958). Reiss and Merling (1958) showed various figures of the toothplate and related structures, and introduced several terms for its specific structures. They described the toothplate to "run always from the intercameral foramen towards the umbilical side for part of the way, turning through torsion towards the dorsal side at their distal ends." Thus the toothplate is convex towards the umbilical center. The rotaliid septal flap, originally proposed by Smout (1954), is also regarded by those authors as an extension of the toothplate, although they retain the term septal flap. Cifelli (1962) suggested the toothplate of *A. beccarii* was not homologous with the original toothplate and he separately called it an axial plate and a lip. He observed that the axial plate is imperforate and the umbilical extension of the plate passes into a chamber flap, without any openings into the umbilical area. The lip, in the different sense of Reiss and Merling (1958), is formed by the axial plate anteriorly projecting through the aperture at the bottom of the septum, except for the final one. Before the recognition of these apertural modifications by these workers, Ishizaki (1943) first noted the morphological difference between the aperture (as the final opening) and the foramen (as the preceding opening). However, he did not refer to any specific anatomical observations.

Based on SEM examination, Seibold (1971) recognized the axial wall as forming a different part of the toothplate in *Ammonia*. Seibold's axial wall and lip correspond to Cifelli's axial plate and chamber flap. Hansen and Reiss (1971) first introduced the concept of a foraminal plate and an umbilical coverplate instead of the toothplate for the rotaliid foraminifera, suggesting the presence of this plate in all chambers, including the final one. They interpreted the septal flap which forms not only the foraminal plate on an axial chamber wall (=previous coil), but also the umbilical coverplate, as showing a continuous lamellar structure. Their observations corroborate Reiss and Merling's explanation. The septal flap consists of an inner lining, which covers the preceding bilamellar septal wall. This lamellar model has been adopted in Lykke-Andersen (1976). Thus the foraminal plate and the coverplate are bilamellar in the original construction. They suggested that the so-called fissure and intraseptal passage are formed as an imperfect adhesion of the septal flap to the preceding chamber. They referred to this fissure as an interlocular space. Müller-Merz (1980) supplied detailed anatomical information on rotaliids and she discussed the apertural structure based on the foraminal plate and cover plate (same sense of umbilical coverplate) model.

Lévy *et al.* (1986) suggested the suprageneric similarities of some rotaliids, including *Ammonia*, to discorbids. They pointed out a similarity in internal structure for which they used the term paries proximus instead of the toothplate. They describe "It (=paries proximus=toothplate) is a thin plate which divides from the septum towards the umbilical face and which constitutes an oblique groove-like fold, instead the chamber, joining the preceding coil. This plate also spreads backwards, that is, in a proximal direction, closing the edge of the folium of the preceding chamber. In equatorial section we give the name 'retroparies' to the back part of the paries proximus." Their paries proximus and the retroparies correspond to the foraminal plate and umbilical coverplate respectively. Although their proposal to subsume the rotaliids within the discorbids at the family level is rejected by Haynes and Whittaker (1990), based on ontogenetic analyses of umbilical modifications, including canals and fissures, there is a similarity in the structure of paries proximus in both taxonomic groups.

The complexity of the internal structure of *Ammonia* is reflected in these different terms. On the other hand, differing recognition of the internal structure among researchers makes for uneasy interpretations. Hottinger *et al.* (1991) redefined the toothplate, particularly in relation to that of *Pararotalia* (see below). They stressed the presence of their toothplate (s.s.) in *Pararotalia* and its absence in *Ammonia*, indicating a difference in suprageneric classification. Revets (1993) questioned whether the rotaliid toothplate was homologous to the buliminid toothplate. He mentioned "The internal structures in rotaliids are not equivalent to toothplates, rather they all seem to conform to the foraminal plate coverplate concept." His argument originated from the difference between the bilamellar structure of rotaliid walls and the single-layer inner lining origin of the buliminid toothplate. Simple usage of the toothplate thus leads to confusion among researchers. The situation is similar in cassidulinids. Nomura (1983a, b) showed that simply the presence or absence of a toothplate is of little taxonomic value. We should describe the apertural decoration with careful attention to the various parts.

Previous observations on the aperture of *Pararotalia*

The detailed apertural structure of *Pararotalia* has been discussed by Loeblich and Tappan (1957, 1964) and Reiss and Merling (1958), based on its type species *Pararotalia inermis* (Terquem) from the Eocene of Paris Basin. Loeblich and Tappan (1987) described the aperture as interiomarginal and extraumbilical-umbilical, and the foramen as areal with the attachment of the toothplate at the proximal margin of the penultimate chamber. Loeblich and Tappan's toothplate is seemingly used in a broad sense, but they distinguished an umbilical plate (=umbilical coverplate here) and an internal septum from the chamber wall (Loeblich and Tappan, 1957). The umbilical coverplate and the internal septum were recognized as secondary structures which can be broken away in the final chamber. Reiss and Merling (1958) stressed that the toothplate (internal septum and umbilical plate of Loeblich and Tappan) is a primary formed structure, but they regarded the umbilical plate as chamber wall.

As to the toothplate of the Japanese *Pararotalia*, Ujiié (1966) described *P. nipponica* as follows: "tooth plate imperforate, extending from proximal margin of last intercameral foramen to distal (peripheral) margin of aperture, adhering its basal (umbilical) margin on proximal margin of spirothecal wall of last chamber throughout whole chamber-length, developing its upper (dorsal) free part broadly but very thinly in form of spatula with concave face turned to axial side and its upper anterior margin bent inwardly." Interestingly, the spatula-shaped portion of the upper toothplate has been interpreted as dissolved in the penultimate chamber based on a secondary wall which closes up an umbilical slit. His observation is similar to Loeblich and Tappan's umbilical plate formation model. However, a real image of the umbilical slit has not been clearly indicated. It may correspond to the interiomarginal slit of the aperture.

Hansen and Reiss (1971) indicated that the original wall structure of *Pararotalia* is identical to that of *Ammonia*. The umbilical coverplate (umbilical plate of Loeblich and Tappan, 1957) extends back from the foraminal plate to the preceding foraminal plate.

Hottinger *et al.* (1991) showed SEM micrographs of their defined toothplate of *P. inermis*. They describe the toothplate as "originating from the septal flap and connected to the inner ventral chamber wall, an imperforate toothplate extends to the distal chamber wall, attached to the dorsal corner of the primarily interiomarginal, extraumbilical aperture, and protruding with a free, serrated edge into the latter." Their toothplate is associated with a canal, which

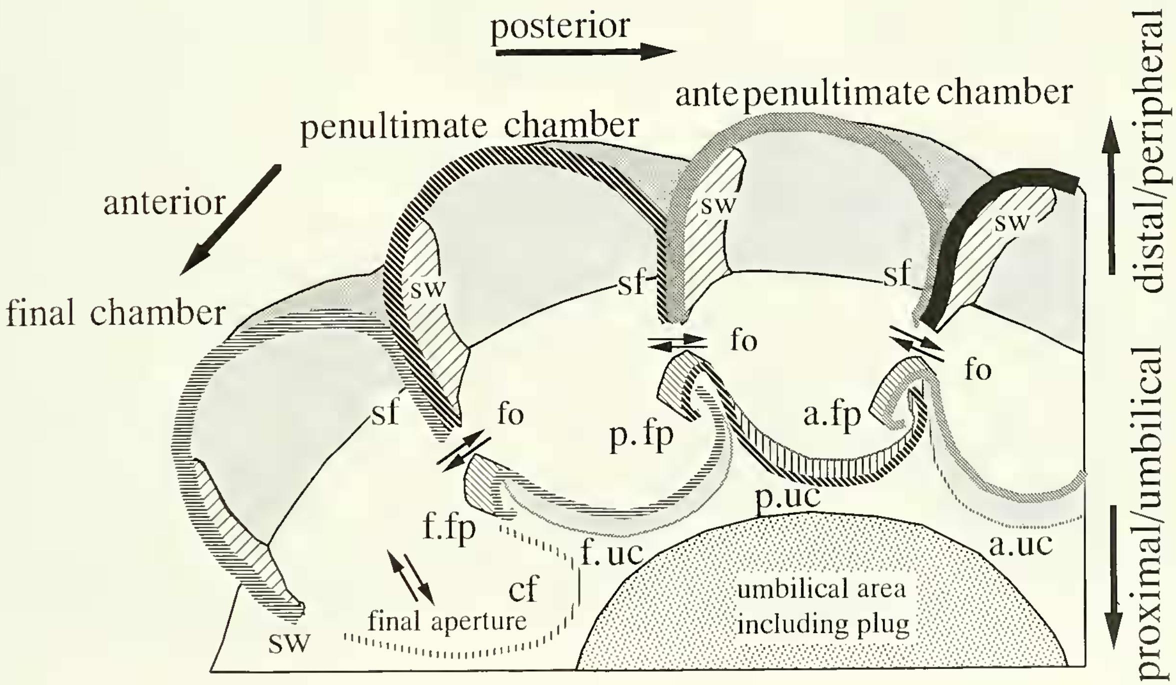


Figure 1. Schematic illustration of internal structure in the genus *Ammonia*. The aperture is an interiomarginal long slit extending from the peripheral side to the umbilicus. The final chamber continues to the foraminal plate and the umbilical coverplate of the penultimate chamber on the umbilical side. Thus, the coverplates around the umbilicus are delayed for one chamber lumen. The so-called toothplate corresponds to the ensemble of foraminal plate and umbilical coverplate. Abbreviations: a.fp=antepenultimate foraminal plate; a.uc=antepenultimate umbilical coverplate; cf=chamber flap; f.fp=final foraminal plate; f.uc=final umbilical coverplate; fo=foramen; p.fp=penultimate foraminal plate; p.uc=penultimate umbilical coverplate; sf=septal flap; sw=septal wall.

communicates with the chamber and with the furrow around an umbilical plug.

Descriptive terms for aperture and its related structure

In order to avoid confusion with respect to the aperture and foramen and their related structures, we use the following terms (Figure 1).

Chamber flap.—Original extension of chamber wall, covering umbilical sutural fissure, decorated with small spines. *Pararotalia* forms an umbilical shoulder associated with nodes on this portion (Loeblich and Tappan, 1957), instead of forming a free chamber flap. [*chamber flap*: Cifelli, 1962] [*chamber lobe*: Parvati, 1971; Haynes and Whittaker, 1990] [*folium*: Hottinger *et al.*, 1991] [*lip*: Hofker, 1950, 1951a, b; Reiss and Merling, 1958; Seibold, 1971; Müller-Merz, 1980] [*umbilical lip*: Ujiié, 1965].

Foramen.—Opening connecting chamber lumina through septa, having a rounded, oval shape. Its shape is different from the final aperture. There are two types of foramen: the *Ammonia*-type and *Pararotalia*-type, based on the position and inclination of the foraminal plate to the walls of previous whorl (Figures 2, 3). [*intercameral foramen*: Smout, 1954][*areal intercameral foramen*: Parvati, 1971][*septal foramen*: Hofker, 1950, 1951a, b]

Foraminal plate.—Anterior plate extended from an umbilical coverplate (Figures 1, 2). It is formed on the proximal side of the aperture, leaving a foramen rounded or oval in shape. The foraminal plate is curled to the posterior out of the foramen, forming a hook-like structure in horizontal section (Figure 2), sometimes it is completely bent, resulting in a columnar shape. This plate usually appears as an isolated plate adjoining the foramen of each chamber, including the final chamber, thereby some authors regarded it as a free structure of the toothplate. Our understanding of this plate agrees with the description of Hansen and Reiss (1971). They suggested that the chamber wall, septal flap, foraminal plate and umbilical coverplate are formed as one continuous structure. The foraminal plate of *Pararotalia* obliquely leans onto the chamber wall of the previous whorl and changes it to a protruded lip (lower lip) (Figure 3) [*anterior projection of umbilical plate*: Parvati, 1971][(apertural) *lip*: Cifelli, 1962] [*foraminal plate*: Hansen and Reiss, 1971; Müller-Merz, 1980; Revets, 1993] [*internal septum*: Loeblich and Tappan, 1957] [*paries proximus*: Lévy *et al.*, 1986] [*toothplate*: Reiss and Merling, 1958; Ujiié, 1965, 1966] [*part of toothplate*: Hottinger *et al.*, 1991]

Hinge.—Junction of the foraminal plate and the umbilical coverplate. It delimits the proximal border or basal border of the foramen. In the *Ammonia*-type foramen, the hinge adheres to the umbilical/proximal side of the apertural opening on the previous whorl (Figure 2), and in the *Pararotalia*-type it adheres to the distal side of the aperture (Figure 3).

Labial aperture.—Opening usually formed on the posterior side of the chamber, except for the final one. Originally this foramen was denoted a protoforamen to distinguish it from a deuteroforamen (Hofker, 1950, 1951a, b). Reiss and Merling (1958) recognized three parts of this aperture, namely, anterior, umbilical, and posterior. However, we recognized it as a single opening in the umbilical coverplate into the upper side of deeply incised sutures or sometimes into the umbilicus. The labial aperture is usually devoid of small spines around its opening. [*protoforamina*: Hofker,

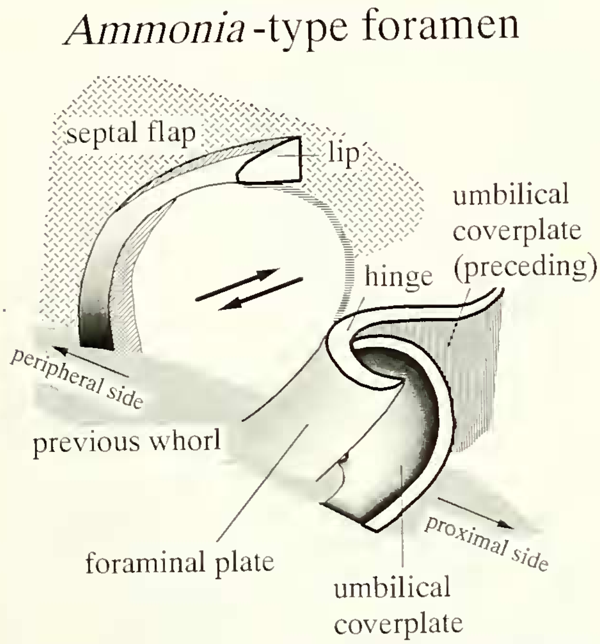


Figure 2. Schematic illustration of *Ammonia*-type foramen. The hinge, junction of the umbilical coverplate and the foraminal plate, butts against the previous whorl. The umbilical coverplate adheres to the preceding foraminal plate or the preceding umbilical coverplate.

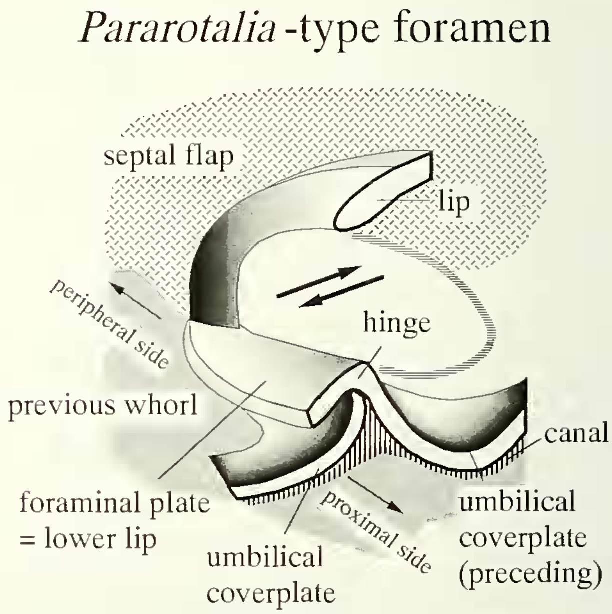


Figure 3. Schematic illustration of *Pararotalia*-type foramen. The hinge, junction of the umbilical coverplate and the foraminal plate, is much inclined toward the peripheral side of the aperture. Thus the foraminal plate appears as a protruded lip on the lower side.

1950, 1951a, b]

Lip.—Plate-like or tube-like structure formed in aperture and foramen. It is distinguished from the lower lip of *Pararotalia*. Sometimes the lip is referred to as the apertural rim.

Lower lip.—Lip usually associated with the foramen of *Pararotalia* and never seen in final aperture. It is formed by an adhesion of the basal part of the foraminal plate to the other, distal side of the final aperture, thereby the foramen of *Pararotalia* is areal. The lower lip is intrinsically the same as the foraminal plate, but structurally different. A toothplate in the sense of Hottinger *et al.* (1991, 1993), which is a different concept from the so-called toothplate, corresponds to our lower lip. To avoid the confused usage of "toothplate," we do not use their toothplate.

Septal attachment.—Attachment of final septal wall to previous whorl, dividing the final aperture into two openings.

Umbilical coverplate.—Wall formed on the umbilical side of each chamber except for the final one, covered with chamber flap, usually forming a labial aperture in *A. japonica* and *A. tepida*, but usually without a labial aperture in *A. beccarii* and *P. nipponica*. This coverplate constitutes the

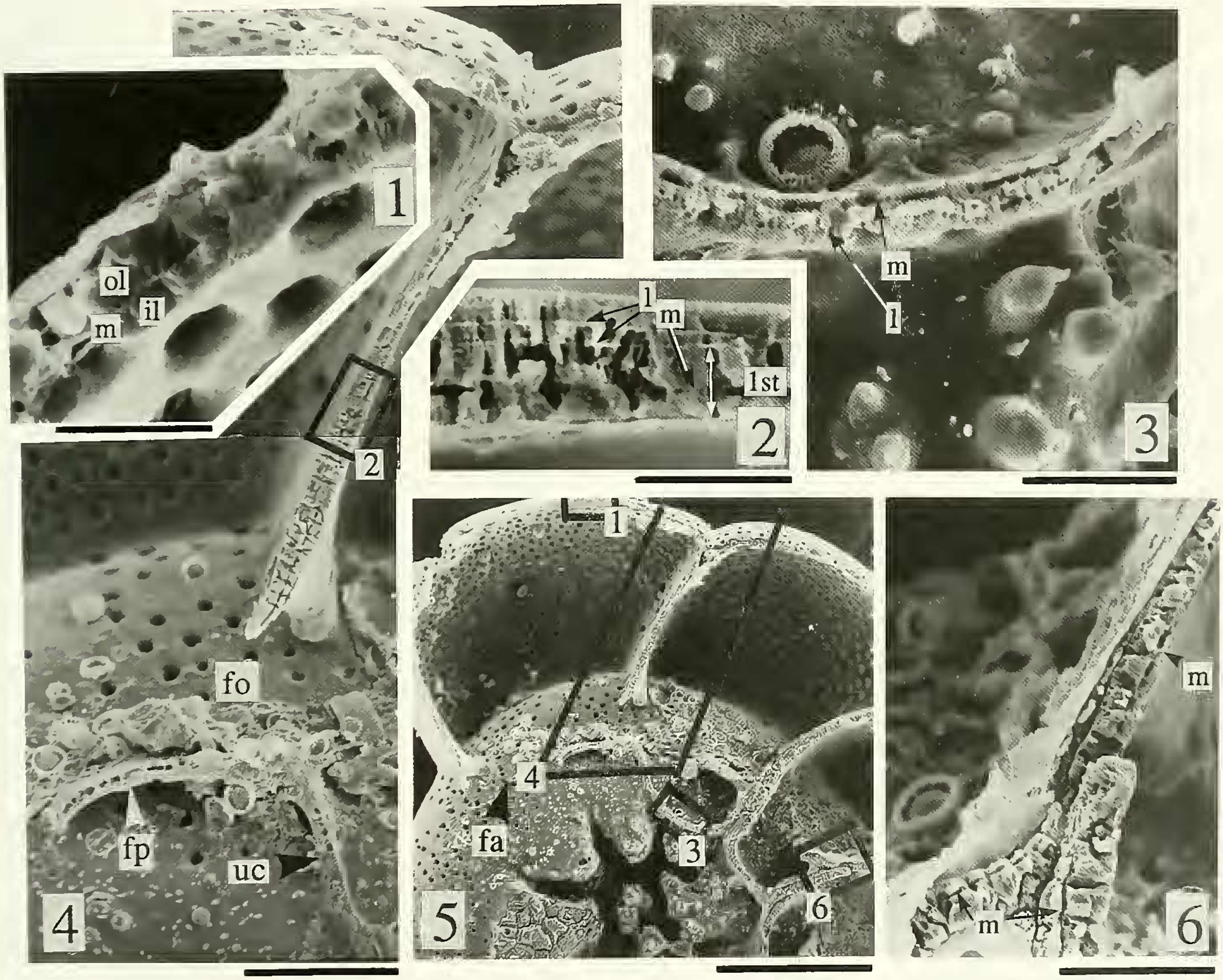


Figure 4. Walls of *Ammonia* sp. etched with 0.5 % phosphoric acid solution showing lamellar structures. **1.** Detail of the final chamber showing the outer layer (ol) and inner lining (il) divided by the incised median layer (m). Scale bar: 5 μm. **2.** Detail of the penultimate septal wall (closeup of no. 4) showing the multiple layers (l) developed on the main bilamellar structure (1st) with the median layer (m). Scale bar: 5 μm. **3.** Detail of the penultimate umbilical coverplate showing a trilamellar structure consisting of the primary bilamellar with median layer (m) and secondary layer (l) (closeup of no. 5). Scale bar: 5 μm. **4.** Detail of the penultimate septal wall, the penultimate foramen (fo), the final foraminal plate (fp), and the final umbilical coverplate (uc). Scale bar: 23.1 μm. **5.** Opened umbilical side of the final and the preceding chamber walls. fa=final aperture. Scale bar: 75 μm. **6.** Detail of the junction of the antepenultimate septal wall, the foraminal plate, and the umbilical cover plate (closeup of no. 5). m=median layer. Scale bar: 7 μm

main part of the umbilical side of the chamber lumen and encloses the preceding foraminal plate. The foraminal plate should be an anterior projection of this coverplate. The foraminal plate lies within every chamber lumen, but the umbilical coverplate is located in the umbilical side of the preceding chamber. The umbilical coverplate is inclined to the previous whorl of the test, making a canal between the plate and the previous whorl in *Pararotalia*. [*axial plate*: Cifelli, 1962] [*cover plate*: Müller-Merz, 1980] [*umbilical coverplate*: Hansen and Reiss, 1971; Revets, 1993] [*part of umbilical plate*: Parvati, 1971] [*retroparies*: Lévy *et al*., 1986] [*umbilical plate*: Loeblich and Tappan, 1957]

Lamellar structure

The final chamber wall of *Ammonia* sp. etched with phosphoric acid solution is typically bilamellar, consisting of inner and outer calcareous lamellae, and a middle incised lamella (in the sense of a primary organic membrane where calcification takes place; Hemleben *et al*., 1977) (Figure 4.1, 4.5). Both the inner and outer calcareous lamellae extend back to cover the penultimate wall, but only the inner lining of the bilamellar structure is superimposed on the outer lamella of the penultimate septal wall, forming a septal flap (Smout, 1954). Such a lamellar structure has been illustrated by Hansen and Lykke-Andersen (1976). In addition to this model, we found multiple lamellae (originally bilamellar with an additional two calcareous lamellae) in the penultimate septal wall near foramen (Figure 4.2, 4.4, 4.5), indicating that the preceding septal wall is not always three calcareous lamellae consisting of original bilamellar plus secondary lamella (= inner lining). This feature is not in agreement with the statements of Hansen and Lykke-Andersen (1976) and Hottinger *et al.* (1991), who noted a trilamellar structure for the preceding septal wall. Their demonstrations follow a typical model of layering. However, the secondary lamellae of the preceding septal walls are variable in different portions. Thus, it matters whether the section looked at was from the umbilicus or spiral side of the test. Our demonstration of multiple lamellae is based on a section from umbilical side of the test (Figure 4.5).

The final foraminal plate is very thin but clearly shows the bilamellar structure. The additional layering does not occur on the final and preceding foraminal plate, which keeps the wall in thin condition. The umbilical coverplate is originally bilamellar, connecting to the foraminal plate in the hinge, but this coverplate has additional layering. Figure 4.3 shows the trilamellar wall of the rudimentary umbilical coverplate consisting of the original bilamellar wall covered with a new secondary lamella. Although we morphologically defined the two apertural types in *Ammonia* and *Pararotalia*, the lamellar structure of the foraminal plate and umbilical coverplate of the *Pararotalia nipponica* is the same as observed in *Ammonia*.

The lamellar structure at the junction of the foraminal plate, umbilical coverplate and preceding septal wall is very

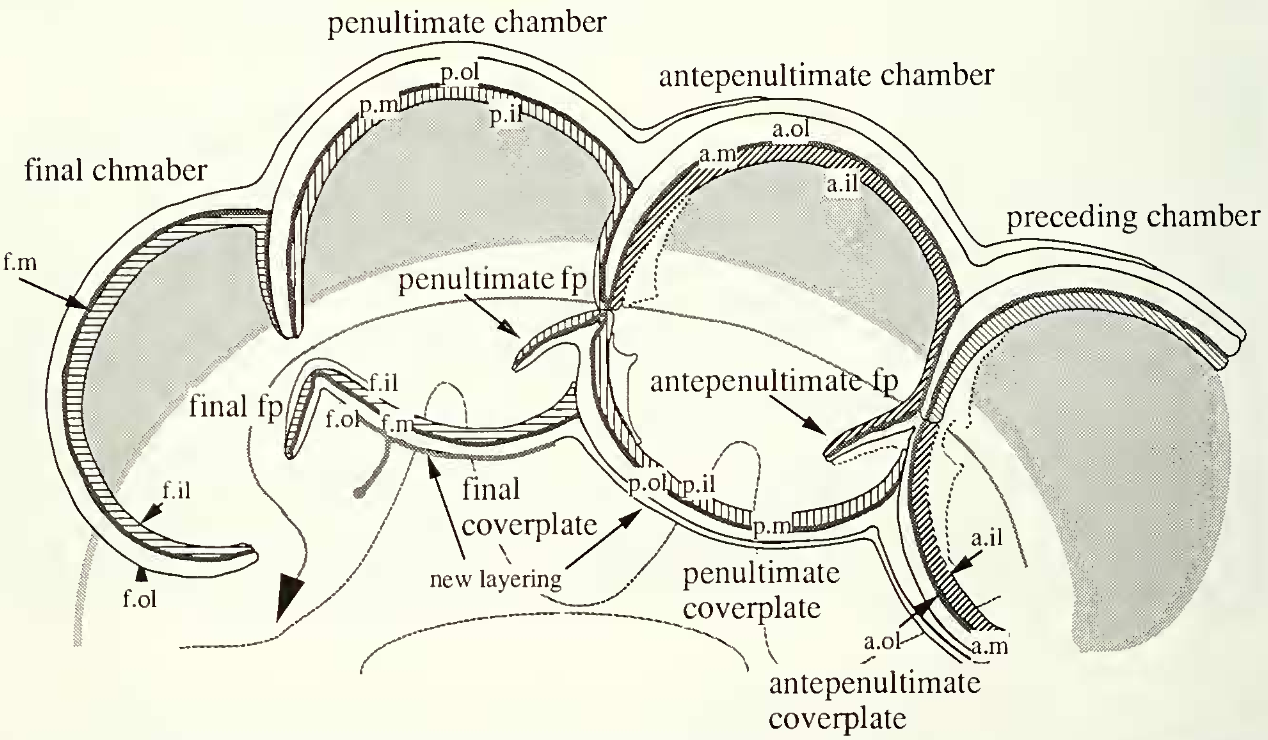


Figure 5. Schematically illustrated lamellar structure in the various parts of the last four chamber walls. Abbreviations: a.il=antepenultimate inner lining; a.m=antepenultimate median layer; a.ol=antepenultimate outer lamella; f.il=final inner lining; f.m=final median layer; f.ol=final outer lamella; p.il=penultimate inner lining; p.m=penultimate median layer; p.ol=penultimate outer lamella; fp=foraminal plate.

complicated (Figure 4.5, 4.6). The inner lining of the foraminal plate connects to the septal flap and the inner lining of the umbilical coverplate connects to the preceding inner lining of the septal wall. In Figure 5, the continuity and discontinuity of each lamella in various portions of the last four chambers are schematically illustrated. This lamellar model is similar to that of Hansen and Lykke-Andersen (1976), except for the median layer of the septal wall illustrated as a discontinuous layer at the junction area.

Description of apertural structures

Ammonia sp.

Figures 2, 4.1–4.6, 6.1–6.8, 7.1

Materials.— Over 10 specimens of *Ammonia* sp. from Recent sediment of brackish Lakes Shinjiko and Nakaumi, Japan. This form has been recognized as a major form of *Ammonia* in Japan, and is identical to *A. beccarii* forma A (Takayanagi, 1955, p. 44, text-figs. 31a–c, in part) and to *A. beccarii* forma 1 (Matoba, 1970).

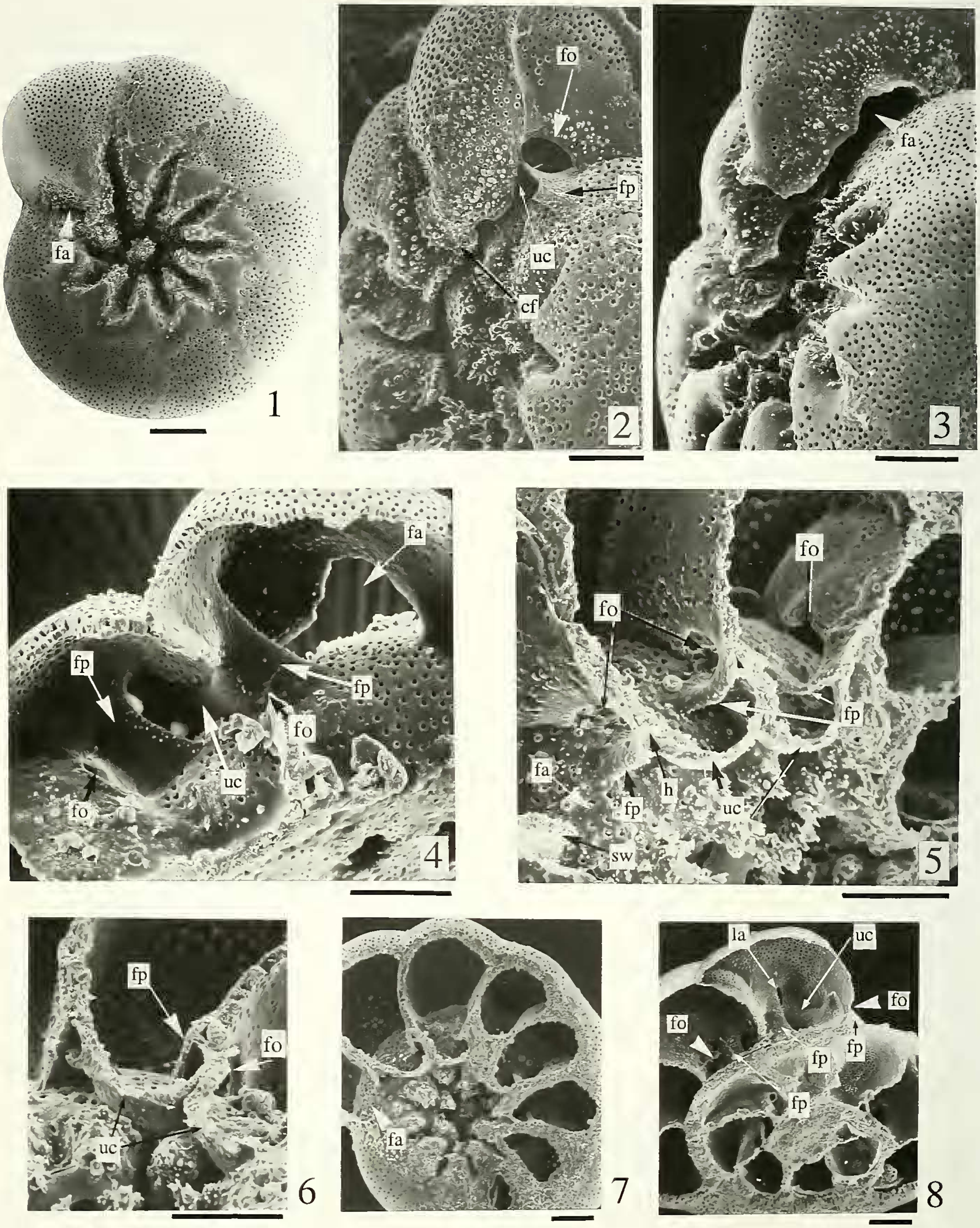
Diagnosis of test.— The specimens are characterized by having nine to ten chambers in the final whorl, with an open umbilicus without a distinct plug, but with numerous spines in and around the umbilicus. Umbilical side of the test is flat or somewhat concave; spiral side is gently inflated. Periphery rounded, very slightly lobulate. Sutures are limbate and slightly inflated on the spiral side, but limbate and incised on the umbilical side. Imperforate chamber flap, associated with spines for each chamber, is developed and each flap is imbricated, covering the incised suture near the umbilicus. Chambers are transparent with numerous fine pores.

Apertural structures.—The final interiomarginal apertural opening is large without any free structure outside the aperture (Figure 6.1, 6.3). Thus the new foraminal plate is only formed between the foramen and proximal side of the finally formed chamber (Figure 6.2–6.4). When the new chamber is formed, the foraminal plate is usually covered with a new umbilical coverplate, which also covers the apertural opening (Figures 6.4–6.7, 7.1). Both the foraminal plate and umbilical coverplate are formed in a series of proximal side walls of the preceding chamber (Figure 6.5, 6.6). The foraminal plate is left, without further development in the chamber lumen, which shows a hook-like structure when observed in horizontal section (Figure 6.5). The umbilical coverplate is less perforate (Figure 6.4), sometimes forms a very small labial aperture (Figure 6.8). However, this is not significant for this species. Chamber flaps are decorated with small spines, imbricated around the depressed umbilical center, and they are not fused with each other (Figure 7.1). Sutures are always incised, having a fissure shape, but they do not form canals.

Remarks.—The examined species has been previously identified as *Ammonia beccarii* (Linné) by Japanese micropaleontologists. We doubt the taxonomic status of this species. *Ammonia beccarii* was originally collected from beach sands of the Adriatic Sea at Rimini, Italy. The type description given by Linné (1758) is not very helpful. In many subsequent works, *A. beccarii* has been broadly interpreted as possessing wide variations in the test morphology. Cushman (1928) recognized three forms in *Ammonia beccarii*, which represent the different generations of this species. Thereafter Japanese micropaleontologists have used this taxonomic name for widely varied forms of *A. beccarii*. However, we cannot accept such forms in the Japanese *beccarii*. Typical *Ammonia beccarii* is characterized by a large test with well developed sutural knobs and fluted sutures on both dorsal and ventral sides. The number of chambers in the final whorl is about 13 chambers in *A. beccarii*, while the Japanese form has a smooth test surface without sutural knobs and usually less than 10 chambers in the final whorl. Thus the Japanese form is quite different from the typical form of *A. beccarii*. With respect to such morphological variation, Walton and Sloan (1990) recognized three different morphotypes in *Ammonia beccarii*. The Japanese form without the umbilical plug falls within the morphological range of their forma *tepida* and the form with the umbilical plug falls within the range of forma *parkinsoniana*. Schnitker (1974) based on the culturing of *Ammonia* and Walton and Sloan (1990) based on geographic distribution suggested a possible morphologic gradation between forma *tepida* and forma *parkinsoniana*, but no such clear gradation has been found between forma *beccarii* and the morphotypes *tepida* and *parkinsoniana*. Ecological observations show that *A. beccarii* (s.s.) and *A. tepida* have different morphofunctional adaptations to their habitats and environments (Debenay *et al.*, 1998). According to Debenay *et al.* (1998), *A. beccarii* (s.s.) lives on some algae as epiphytic life, whereas *A. tepida* lives in brackish sediments as endopelic life. The Japanese *A. beccarii* is similar to their *A. tepida*. Poag (1978) and Walton and Sloan (1990) mentioned that the geographic distribution of the typical form of *A. beccarii* (s.s.) appears to be limited to the Mediterranean, the eastern Atlantic coast and the western Atlantic coast from Florida to Nova Scotia. Whittaker (personal comm.) suggested that true *A. beccarii* lives only in the Mediterranean Sea and does not occur outside of it. These views are biogeographically supported, as no similarities exist between the Mediterranean fauna and the Indo-Pacific fauna (Rögl and Steiniger, 1984). Thus, no typical live or fossil *A. beccarii* occurs in and around Japan. This means the Japanese form does not represent *Ammonia beccarii* (s.s.).

Another problem in the systematics of *Ammonia beccarii* is introduced from DNA analysis. Pawlowski *et al.* (1995) showed a high similarity of the ribosomal DNA sequences between *A. beccarii* (s.s.) and the Japanese "*A. beccarii*." The Japanese form they examined in their DNA study is the same as we morphologically examined. Our morphologic comparison, however, indicates a taxonomic difference between the two entities. The different results arrived at by morphological comparison and molecular analysis cannot be reconciled at this time.

For these reasons, we hesitate to identify the Japanese form as *A. beccarii*, despite its being a well known species in brackish and shallow waters.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Ammonia japonica (Hada)

Figure 7.2–7.5

Type reference.—*Rotalia japonica* Hada, 1931, p. 137, text-figs. 93a–c.

Materials.—*A. japonica* (Hada) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea of Japan.

Diagnosis of test.—Examined specimens are characterized by an inflated test with nine to ten chambers. Chambers are wedge-shaped toward the umbilicus. An umbilical plug is not usually developed in this species. The chamber flaps are less developed than in *Ammonia* sp. Radiate sutures on both the umbilical and spiral sides are straight. Umbilical sutures are incised and decorated with fine spines.

Apertural structures.—The final aperture is divided into two openings by the septal attachment (Figure 7.2–7.5). The anterior aperture is interiomarginal, with an arch-shaped opening and the posterior one is not easily seen, as it is covered by the chamber flap, but its shape is arched (Figure 7.4). The lip is somewhat protruded. The foraminal plates are curled and protrude out of the foramen when observed in horizontal section (Figure 7.3, 7.5). The foraminal plate without a free structure extends to form the ventral chamber wall in the final chamber (Figure 7.4). The umbilical coverplate is formed under the chamber flap when a new chamber is formed, but remains open in the upper part of the final aperture, forming a rounded labial aperture for each chamber but the final one (Figure 7.5). The chamber flap is triangular and points to the umbilicus and becomes larger as a new chamber is added, covering the labial aperture. Ventral sutures with small spines are deeply incised toward the umbilicus, like a fissure.

Remarks.—*Ammonia japonica* is morphologically distinguished from *Ammonia* sp. by having straight, radiate sutures on the dorsal side and a more inflated test. Development of the septal attachment is another characteristic feature of this species which distinguishes it from allied species. *Ammonia inflata* should be allied to *A. japonica* in having straight radiate sutures.

Ammonia sp.cf. **_A. parkinsoniana_** (d'Orbigny)

Figure 7.6–7.8

Type reference.—Cf. *Rosalina parkinsoniana* d'Orbigny, 1839, p. 99, pl. 4, figs. 25–27.

Materials.—Several specimens of *Ammonia* sp. cf. *parkinsoniana* from Recent sediment of brackish Lake Nakaumi.

Diagnosis of test.—Examined specimens are characterized by a thick lenticular test, having a distinct umbilical plug (Figure 7.6). The size is smaller than the examined form of *Ammonia* sp. The umbilical area is less decorated by spines and compact. The umbilical and spiral sides are inflated and the nonlobulate periphery is subacute. Chambers are eight to nine on the umbilical side and less inflated. Sutures on umbilical side are less incised and the ones on the spiral side are distinctly limbate for the test size. Walls are transparent with numerous fine pores and the test walls are brown in color.

Apertural structures.—The test morphology of *Ammonia* sp. cf. *A. parkinsoniana* differs from that of *Ammonia* sp. in having an umbilical plug and a small and more compact test. However, the apertural structure is very similar to that of *Ammonia* sp. (Figure 7.7, 7.8). The major difference is found in the less developed chamber flap (Figure 7.7). The final aperture is interiomarginal, mostly covered with a small chamber flap (Figure 7.7). The base of the foraminal plate adheres to the previous whorl and extends rearward to contact the umbilical coverplate. The umbilical coverplate covers the final apertural opening, leaving a rounded foramen (Figure 7.7). No labial aperture is formed in this species. Thus the foraminal plate is concealed by the umbilical coverplate, and remains in a plate-like structure in the preceding chamber lumen.

Remarks.—This form is identical to the form having the umbilical plug in *A. beccarii* forma 2 (Matoba, 1970, p. 48, pl. 5, figs. 11a–c, in part). Despite having the umbilical plug, this form is different from *Ammonia. beccarii* (s.s.) on account of its small test and smooth test walls. According to Walton and Sloan (1990), this form falls within the range of morphotypic variation of *Ammonia beccarii* forma *parkinsoniana*. We tentatively identified this examined form with *Ammonia*. sp. cf. *A. parkinsoniana*, pending further comparison with the type species.

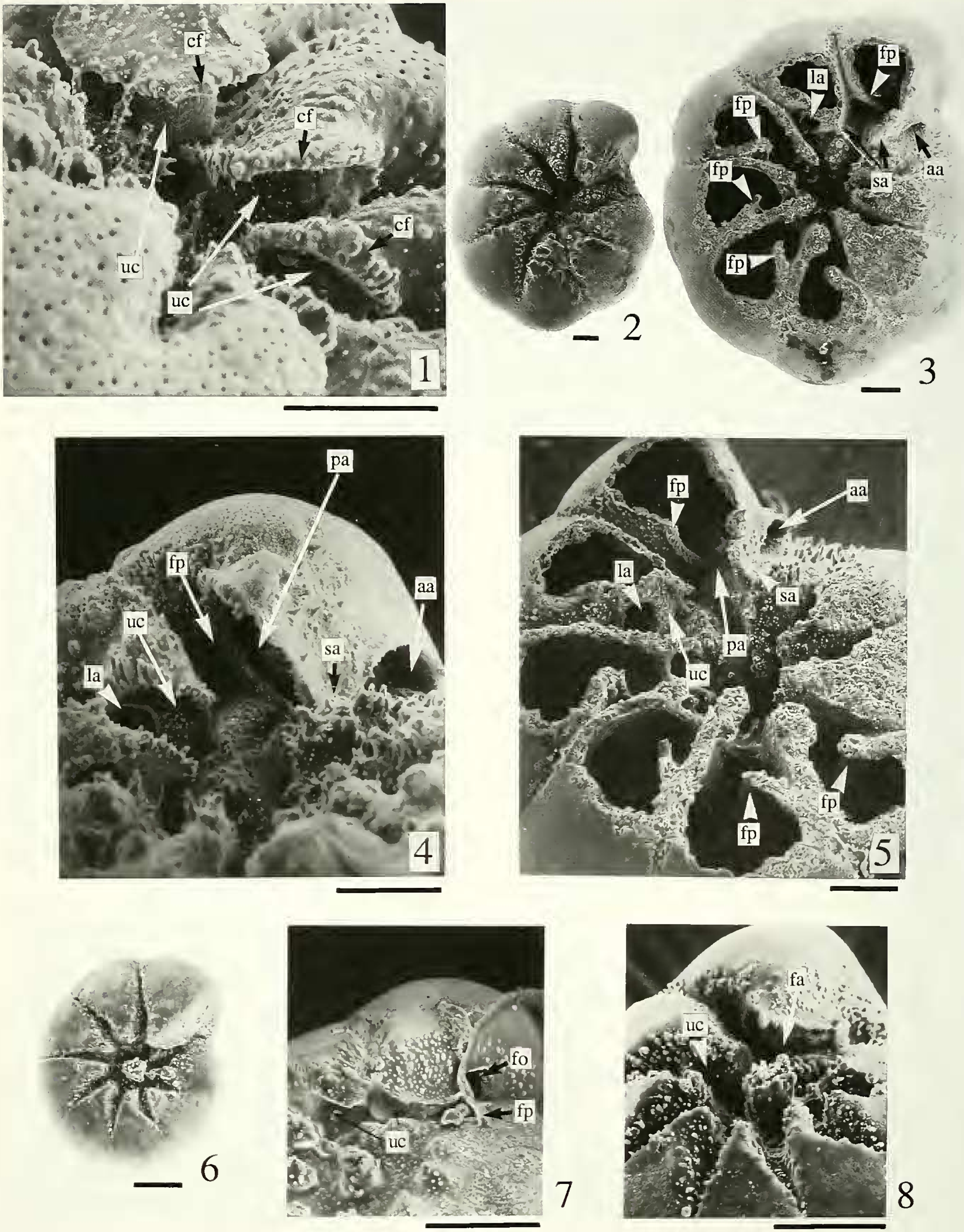
Ammonia tepida (Cushman)

Figure 8.1–8.3

Type reference.—*Rotalia beccarii* (Linné) var. *tepida* Cushman, 1931, p. 61, pl. 13, figs. 3a–c.

Materials.—*Ammonia tepida* (Cushman) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea

Figure 6. External and internal apertural structure of *Ammonia* sp. Scale: 50 μm. **1.** Umbilical side view. This form mostly has an open umbilicus. Fine umbilical plug is shown, but it is usually indistinct in optical observation. **2.** Oblique view of the umbilical side. The final chamber is removed, thus the penultimate foramen and the foraminal plate can be seen. The umbilical coverplates cannot be seen because they are concealed by the chamber flaps. **3.** Oblique view of the umbilical side. The final aperture is an interiomarginal slit from the peripheral side to the umbilicus. Note long slit of the apertural opening is different from rounded intercameral opening. **4.** Internal features of the final and penultimate chambers. Spiral side of walls is removed. Walls of the foraminal plate and the umbilical coverplate are smooth. **5.** Opened umbilical side showing the foraminal plates and the umbilical coverplates convex towards the umbilicus. The umbilical coverplate adheres to the hinge of the preceding foraminal plate and umbilical coverplate. **6.** The umbilical coverplate convex toward the umbilicus. The umbilical coverplate is curled and butts against the previous chamber whorl. **7.** External view of the opened umbilicus. **8.** Spiral side walls removed. Foraminal plate and umbilical coverplate shown in the penultimate chamber. Very small labial aperture may be seen in this specimen, but it is usually rare. Abbreviations: cf=chamber flap; fa=final aperture; fp=foraminal plate; h=hinge; fo=foramen; la=labial aperture; sw=septal wall; uc=umbilical coverplate.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of Japan.

Diagnosis of test.—This species has a small test for this genus and has six to seven chambers in the final whorl. The umbilicus is depressed, without a plug. Sutures incised and decorated with small spines on the umbilical side and flush with surface on the spiral side. Ventral chambers are broad and oval. Chamber flaps are developed, imbricated, and cover the sutures near the umbilicus.

Apertural structures.—The final aperture is interiomarginal and consists of a single opening extending to the umbilicus, with the developed chamber flap (Figure 8.1). The foraminal plate is formed on the proximal side of the foramen (Figure 8.2), and the hinge is much inclined and curled to connect to the posterior part of the chamber flap. Thus the posterior part of the chamber flap is concave where the labial aperture is formed except for the final chamber (Figure 8.1). The labial aperture is rather large and rounded in shape, which can be seen from a posterior oblique view (Figure 8.3). The umbilical coverplate is completely covered with the chamber flap, but always developed except in the final chamber (Figure 8.2).

Remarks.—Seibold (1971) put *A. tepida* in the genus *Discorbis*, based on differences of the internal structure such as the relationships between the toothplate (=foraminal plate), axial wall (=umbilical coverplate here), and septal lamellarity (that is, single or double). That idea is invalid, because these internal structures are not characteristic of *Discorbis*, but of *Ammonia*.

Lévy *et al.* (1986) pointed out no critical differences in the internal structure between *A. beccarii* and *A. tepida*. However, the development of the large labial aperture of *A. tepida* is not only significant in distinguishing this species from *A. beccarii*, but also from our examined *Ammonia* sp. herein. All examined specimens are in accordance with Cushman's original concept of *Ammonia beccarii* var. *tepida* (s.s.) and represent the typical *Ammonia beccarii* forma *tepida* of Walton and Sloan (1990). Although there are externally gradational morphologies in Walton and Sloa n's forma *tepida*, our *tepida* is different from the other end member form (e. g., *Ammonia* sp. herein) in the presence of the labial aperture. *Ammonia tepida* may represent a definite species as suggested by Pawlowski *et al.* (1995). We are of the opinion that forma *tepida* of Walton and Sloan (1990) needs further consideration based on observations of the internal structure.

Ammonia tochigiensis (Uchio)

Figure 8.8, 8.9

Type reference.—*Rotalia tochigiensis* Uchio, 1951, p. 374, pl. 5, figs. 1a–c.

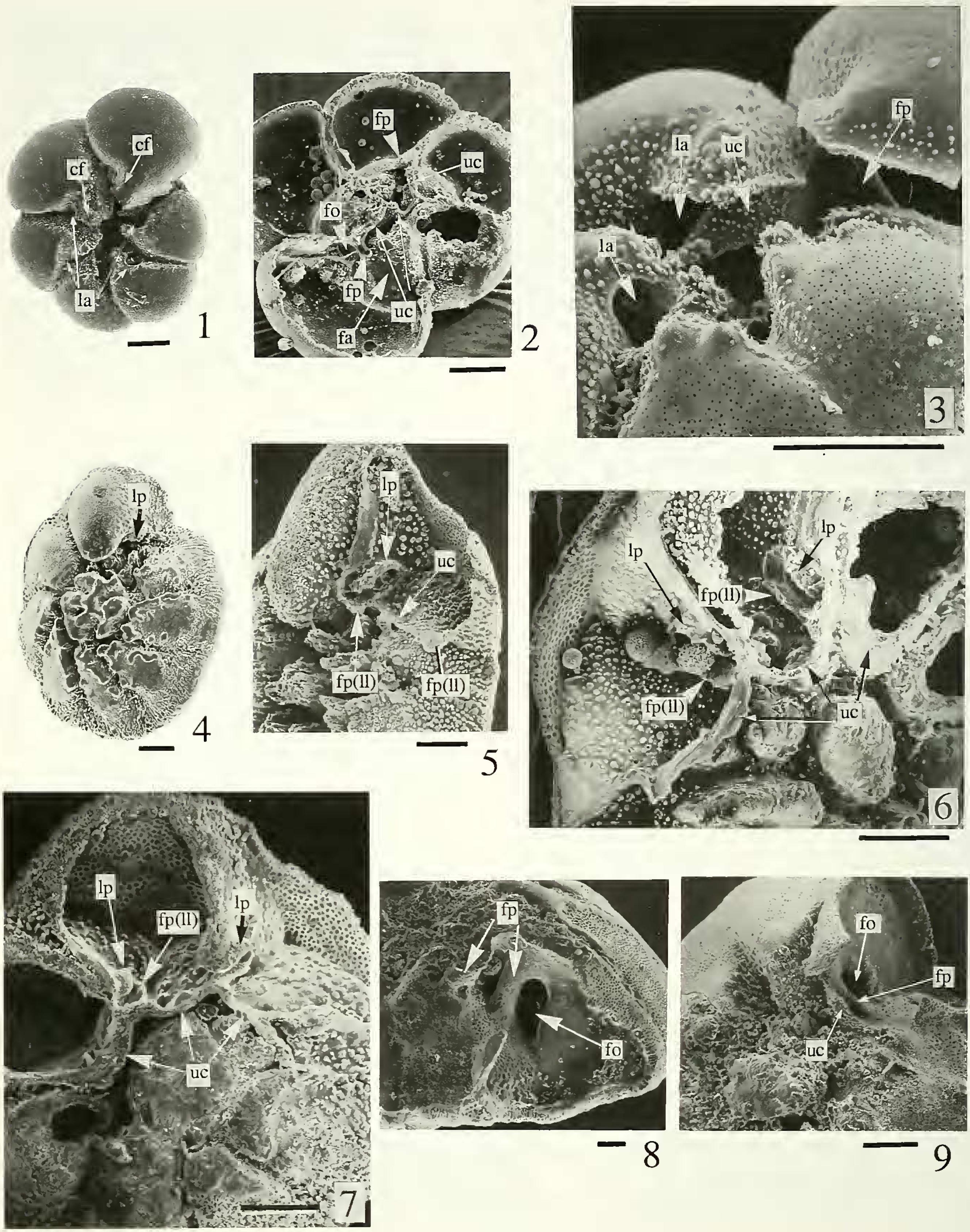
Materials.—One examined specimen from the type locality of this species, the Momiyama Formation, Tochigi Prefecture; five specimens from the Miocene Bihoku Group, Southwest Honshu, Japan. This species is very common in early middle Miocene shallow deposits of Japan.

Diagnosis of test.—Most examined specimens are naturally broken, without the final chamber, but well preserved specimens show the interiomarginal aperture. An umbilical plug is distinctly developed. Chamber flaps are less developed, thus chambers around the umbilical plug are serrated. 13–15 chambers in the final whorl. Sutures distinct and limbate on both sides of test and less incised on umbilical side. Sutures on spiral side are raised.

Apertural structures.—The final aperture is interiomarginal, mainly open on the umbilical side, but covered with a less developed chamber flap. The hinge is columnar in shape, formed at a high angle to the preceding whorl near the umbilicus, with a less developed free margin of the foraminal plate (Figure 8.8). The base of the foraminal plate on the previous whorl is strongly bent toward the posterior. The umbilical coverplate adheres to the edge of the preceding foraminal plate, leaving a concave space between the umbilical coverplate and the foraminal plate (Figure 8.9). Labial apertures are found in an incised suture near the umbilicus.

Remarks.—The internal structure with emphasis on the aperture has been discussed by Ujiié (1965). He described exactly the final aperture as showing an interiomarginal-basal narrow slit, but the description with respect to the foramen is unclear. We did not observe such a structure indicating "interiomarginal foramen converted from aperture, probably by partial resorption of apertural face slightly before addition of new chamber." His toothplate structure is not clearly distinguished from the chamber wall or the umbilical coverplate. His description says the free structure (foraminal plate?) is added after the formation of the new chamber. In our view the umbilical coverplate positioned in the penultimate chamber is formed simultaneously with the foraminal plate as well as the final chamber wall.

Figure 7. External and internal apertural structure of *Ammonia* sp., *Ammonia japonica* (Hada, 1931), and *Ammonia* sp. cf. *A. parkinsoniana* (d'Orbigny, 1836). Scale: 50 μm. **1.** Closeup figure of the chamber flaps and the umbilical coverplates in *Ammonia* sp. **2.** Umbilical side view of *A. japonica*. **3.** *A. japonica* with artificially removed chamber walls of the umbilical side. **4.** Oblique view of the umbilical side of *A. japonica*. Proximal part of the septal wall adheres to the previous whorl in its final chamber (septal attachment in here), thus the anterior and posterior apertures are shown. The foraminal plate with its thickened rim represents the posterior end of the final chamber. **5.** Oblique view of the umbilical side of dissected *A. japonica*. The posterior aperture changes into the labial aperture with development of the umbilical coverplate. **6.** Umbilical side view of *A.* sp. cf. *A. parkinsoniana*. **7.** Oblique view of the umbilical side of *A.* sp. cf. *A. parkinsoniana* without the final chamber. The umbilical coverplates seal the previous interiomarginal apertures. 8. Oblique view of the umbilical side of *A.* sp. cf. *A. parkinsoniana* showing opening of final aperture. No labial apertures are shown. Abbreviations: aa=anterior part of aperture; cf=chamber flap; fa=final aperture; fp=foraminal plate; fo=foramen; la=labial aperture; pa=posterior part of aperture; sa=septal attachment; uc=umbilical coverplate.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Pararotalia nipponica (Asano)

Figures 3, 8.4-8.7

Type reference.—*Rotalia nipponica* Asano, 1936, p. 614, pl. 31, figs. 2a-c.

Materials.—*Pararotalia nipponica* (Asano) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea of Japan.

Diagnosis of test.—The specimens examined are characterized by a well developed umbilical plug. Eight chambers on the umbilical side, inflated without a chamber flap, and having a rounded triangular shape around the umbilical plug. Sutures on the umbilical side are mostly radiate, deeply incised, but those on the spiral side are tangential. Umbilical spiral suture is covered with overhanging chambers (=umbilical shoulder), but it is never sealed up by the umbilical shoulders.

Apertural structures.—The final aperture is an interiomarginal slit, extending from the midbase of the apertural face to the umbilicus (Figure 8.4). The lip is thick and protruded. The chamber flap is undeveloped, thus the umbilical canal and sutural grooves are well shown as deep fissures on the umbilical side. The foraminal plate is only associated with the foramen and the base of its hinge adheres to the distal end of the preceding apertural opening, thereby forming the protruded lip (Figure 8.5-8.7), which is here called the lower lip (Figure 3). Thus the foramen is areal in position (Figure 8.5). The umbilical coverplate is developed around the umbilical plug except in the final chamber and connects to the foraminal plate (Figure 8.6, 8.7). No openings corresponding to a labial aperture are found in the umbilical coverplate, indicating the foramen is the main passage between the chambers.

Remarks.—The previously described toothplate of this species is morphologically very ambiguous and confused. The toothplate of Ujiié (1966) may correspond to the umbilical coverplate, according to his description and sketched figures (see above). He noted the umbilical slit (=aperture in original form) is closed with secondary calcification, and then the free toothplate disappears. Because of the absence of such a free structure in the penultimate and preceding chamber, he considered this to indicate partial dissolution of the toothplate. However, such an ingenious explanation is unnecessary. Originally, there are no free structures comparable to his suggested structure in *P. nipponica*.

External test shape of *Pararotalia nipponica* is similar to that of *P. inermis*. We can observe the protruded structure demonstrated by Hottinger *et al.* (1991) on the umbilical side of *nipponica*'s foramen. This free part of the walls, which is called a toothplate by them, is structurally the same as the lower lip. We find also this type of foramen in *Neorotalia*, as can be seen in the detailed figures of Hottinger *et al.* (1991, 1993).

Discussion

Our observations suggest that the foraminal plate and umbilical coverplate complexes are variable at species level. Moreover, the interrelationships of these plates with neighboring structures are too complicated to easily understand without detailed anatomical observations. Thus, the simple application of the presence or absence of the so-called toothplate to taxonomic decisions is not a reliable criterion.

The foraminal plate and umbilical coverplate are a specified part of the chamber wall formed simultaneously in association with the preceding foramen. On this point, the final aperture is connected with the preceding foramen via the foraminal plate, which may be apparently correlated with the original toothplate concept of Hofker (1950, 1951a, b). Nevertheless, the critical point is that the foraminal plate involves both the final aperture and the preceding foramen. The umbilical coverplate serves only to seal the preceding apertural opening and is not associated with the formation of the final chamber wall. Such foraminal plate and umbilical coverplate structures are characteristic of the rotaliids, not of other taxa with a toothplate. The buliminid toothplate extends within the chamber lumen and no parts of it are concerned with the preceding chamber (e. g., Hofker, 1950, 1951a, b; Revets, 1989). We regard this difference of the toothplate as of primary importance in distinguishing the rotaliid aperture from others. Thus we follow the foraminal plate and umbilical coverplate concept of Hansen and Reiss (1971) and Revets (1993), who stressed the significance of applying only the terms foraminal plate and coverplate to rotaliid taxonomy rather than accepting the general toothplate concept.

Figures 8. External and internal apertural structure of *Ammonia tepida* (Cushman, 1931), *Ammonia tochigiensis* (Uchio, 1951), and *Pararotalia nipponica* (Asano, 1936). Scale: 50 μm. **1.** Umbilical side view of *Ammonia tepida* . Note well developed chamber flaps. **2.** Oblique view of the umbilical side of dissected *A. tepida*. The umbilical coverplates adhere to the preceding umbilical coverplate, apart from the hinge in this species. **3.** Umbilical side view of *A. tepida* indicating the foraminal plate, umbilical coverplate, and labial aperture. **4.** Umbilical side view of *P. nipponica* . The final aperture is an interiomarginal slit extending from the peripheral side to the umbilicus. **5.** Oblique view of the umbilical side of dissected *P. nipponica*. The antepenultimate aperture is an oval surrounded by the lip and the lower lip (=foraminal plate). The remnant of the dissected penultimate chamber wall shows the lower lip linking to the umbilical coverplate. **6.** *P. nipponica* with removed chamber walls of the umbilical side showing the lower lips and the umbilical coverplates. The lower lips represent the foraminal plates as a continuation to the umbilical coverplates. **7.** Umbilical side view of *P. nipponica* with the final three chambers removed. The continuous structure of the lower lip (=foraminal plate) and the umbilical coverplate is clearly shown. The umbilical coverplates adhere to the previous whorl at a low angle. **8.** Peripheral view of dissected *A. tochigiensis*. Columnar-shaped foraminal plate is due to a posterior bend of the plate. The umbilical coverplate adheres to the bent edge of the preceding plate. **9.** Oblique view of the umbilical side of dissected *A. tochigiensis*. The complex of foramen, foraminal plate and umbilical coverplate is shown in the antepenultimate chamber. Abbreviations: cf=chamber flap; fa=final aperture; fp (ll)=foraminal plate (lower lip); fp=foraminal plate; fo=foramen; la=labial aperture; uc=umbilical coverplate; l=lip.

On the other hand, different opinions appeared in the discussion and description of the rotaliids by Hottinger *et al.* (1991, 1993). They are consistent in using the term toothplate by revising its concept. In addition to the original concept, their toothplate includes a new point of view such as an association with a canal. They defined the toothplate as "A toothplate separates partly or entirely the main chamber lumen from an axial space....Interconnected toothplates produce a primary canal." According to their definition, *Pararotalia* is associated with a toothplate as it has an umbilical canal, while *Ammonia* is not associated with a toothplate as it has no umbilical canal. The presence or absence of their toothplate is due to whether the canal is formed or not. Their toothplate concept in relation to structures such as foraminal plate, umbilical coverplate and umbilical plate is subordinate in significance. As we observed in the aperture of *Pararotalia*, the umbilical coverplate obliquely leans to the walls of the previous whorl. The inclination of the foraminal plate is much the same as the umbilical coverplate and changes to a lip in this type of foramen (Figure 3). Thus we usually observe the canal between the umbilical plate/foraminal plate and the previous whorl of the test. This structural reconstruction is similar to that of *Neorotalia* demonstrated by Hottinger *et al.* (1991, p. 29, figure 7) and *Pararotalia* (Hottinger *et al.*, 1993, p. 141, pl. 200, figs. 10, 11). This means that their toothplate is nothing but our foraminal plate, which is here called the lower lip in order to emphasize the structural difference from the *Ammonia*-type foramen. The same view can be seen in Revets (1993), who stated "The internal structures delimiting the canals are the perfect homologues of the foraminal- and coverplate of *Ammonia*."

In addition to different interpretations for the toothplate among these authors, there are also discrepancies with respect to the lamellar structure. Hansen and Reiss (1971) observed that the foraminal plate is bilamellar. Later, Revets (1993) confirmed the bilamellar structure of the rotaliid genus *Neorotalia*, along with the taxonomic significance of the buliminid toothplate consisting only of a modification of the inner lining. Hottinger *et al.* (1991) state that the septal flap, consisting of the inner lamella (=inner lining), may extend into the foraminal plate, coverplate, and toothplate. Thus an additional inner lamella is imposed on the original bilamellar walls, producing trilamellar walls. A similar view of lamellar structure was suggested by Revets (1993) when he stated "As the coverplate butts into the foraminal plate of the prepenultimate chamber, it covers its outside by a secondary lamella, so that this foraminal plate cum coverplate is trilamellar." Our observations of *Ammonia* sp. indicate, however, that the foraminal plate is always bilamellar and the preceding umbilical coverplate is covered with an outer lamella of newly formed coverplate (Figure 5). The foraminal plates never receive additional lamella from the new umbilical coverplate. We need further comparisons to ascertain the variation in the lamellar structure.

Conclusions

We studied the internal structure of some Japanese species of the genera *Ammonia* and *Pararotalia* to validate Hofker's original concept of the toothplate (Hofker, 1950; 1951a, b). Two major structures, the foraminal plate and the umbilical coverplate (Hansen and Reiss, 1971), are distinguished instead of the general term toothplate. The lamellar structure of the foraminal plate and umbilical coverplate is originally bilamellar. Two types of aperture except for the final one, *Ammonia*-type and *Pararotalia*-type foramen, are recognized, according to the position of the foraminal plate constructed in the aperture. The description of the foraminal plate/umbilical coverplate structure is significant to rotaliid taxonomy in understanding intraspecific morphological variation. However, the structural complex should not be treated as a unit in order to make generic-level distinctions.

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